

Early development of the deep-sea ampharetid (Polychaeta: Ampharetidae) *Decemunciger apalea* Zottoli

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Abstract.—Early development of the opportunistic, deep-sea ampharetid polychaete *Decemunciger apalea* Zottoli is described from specimens removed from wood panels placed on the deep-sea floor by Turner (1973). Larvae with less than 8 setigers were not found. Larval spatulate notosetae and neuropodial uncini on segments 3–6 formed during early development are eventually lost by the 14-setiger stage making segment 7 the first uncinigerous thoracic segment in juveniles and adults. Early development of this species is generally similar to that described for other shallow and deep-sea ampharetids.

The deep-sea ampharetid polychaete *Decemunciger apalea* Zottoli inhabits galleries in wood originally excavated by bivalve molluscs belonging to the genera *Xylophaga* and *Xyloredo* (Family Pholadidae, subfamily Xylophaginae) (Turner 1973, 1977; Zottoli 1982). The wood was placed by R. D. Turner, using the submersible DSRV *Alvin*, at four experimental bottom stations in the North Atlantic to “test the hypothesis that wood is an important source of nutrients and contributes to diversity in the deep-sea” (Turner 1973, 1977). This study is based on a detailed examination of 393 complete juvenile and adult specimens from wood panel N31 (DOS2) (Fig. 1). Early development and further role of this species in deep-sea ecosystems is discussed.

Materials and Methods

Three experimental islands, each with 12, one foot spruce cubes, were placed by Turner (1977), for a period of five years at the following locations: Deep Ocean Station 1 (DOS-1), 39°46'N, 70°41'W, 110 miles south of Woods Hole, Mass., in 1830 m; Deep Ocean Station 2 (DOS-2), 38°18.4'N, 69°35.6'W, 190 miles southeast of Woods Hole, Mass., in 3506 m; Tongue

of the Ocean, Bahama Islands (TOTO Tower 3), 24°53.2'N, 77°40.2'W, in 2066 m.

Each experimental island is surrounded by wood panels (24" × 5" × 1") which are removed and replaced each time the islands are visited. Each panel is enclosed in a mesh bag when it is retrieved, to prevent loss of specimens. The mesh bags and their contents are then transferred to retrieval boxes carried on the DSRV *Alvin* basket. The contents of the bags may be preserved at the time the boxes are closed for return to the surface by puncturing plastic bags containing glutaraldehyde, previously placed in the retrieval boxes. In certain cases, the panels were preserved immediately upon reaching the surface. Wood panel N31 (DOS 2) was submerged by *Alvin* on dive 601, 5 Sep 1975, and removed on dive 777, 3 Aug 1977 harboring 393 whole ampharetids. Refer to Turner (1973, 1977) for a more detailed description of the methods used to place and retrieve the panels from experimental islands.

Systematics

Ampharetid polychaetes are for the most part widest anteriorly, tapering gradually towards the posterior end. The prostomium, a pre-segmental structure, is situated imme-

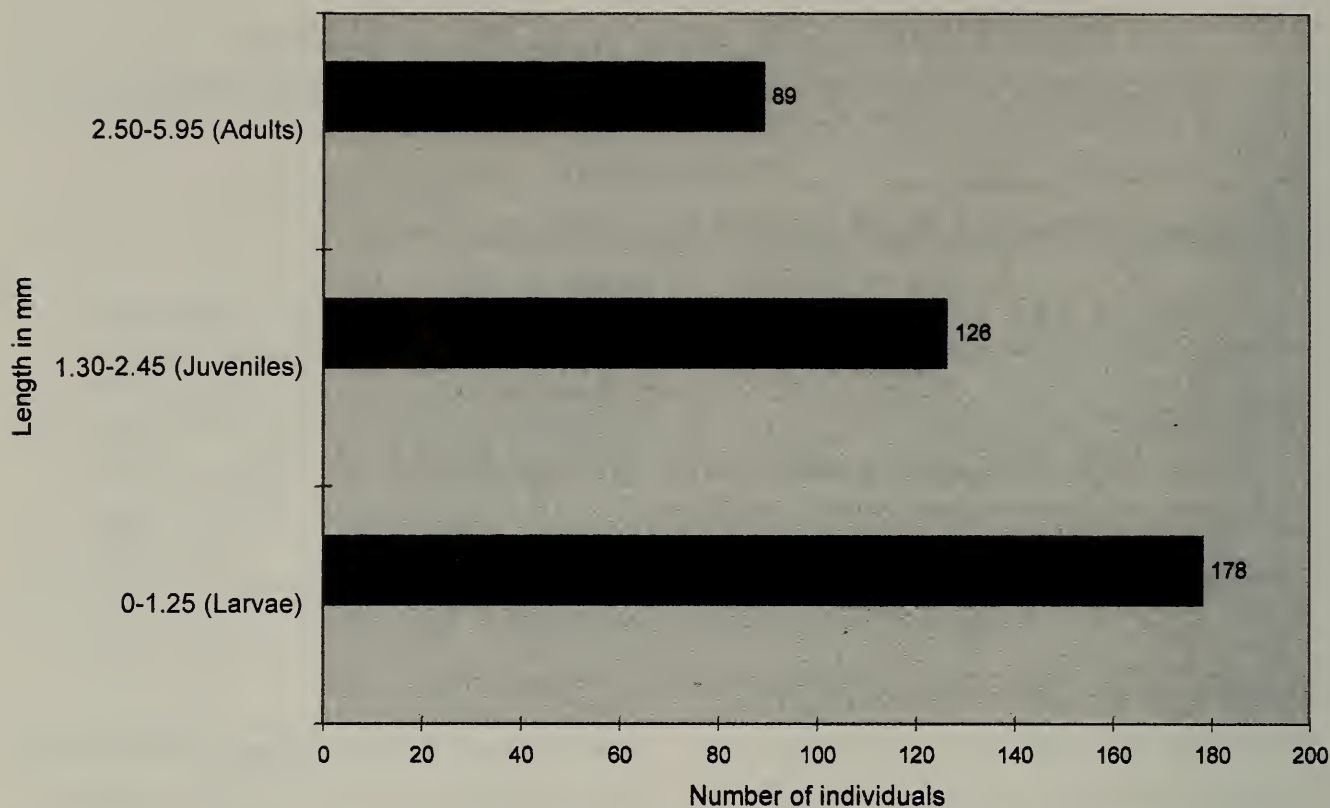


Fig. 1. Frequency histogram for length from a collection of 393 *Decemunciger apalea* from wood panel N31 (DOS2).

diately in front of the peristomium. Segments 1 and 2 that are fused together follow behind the peristomium. Refer to Zottoli (1974) for additional information on the formation of these structures. The segmental numbering system used in this paper is that of Malmgren (1865–1866) and Fauvel (1927) who recognized two segments in front of the paleal segment (segment 3). The thorax begins on segment 4. Segment 3 in some species has one dorsolateral bundle of paleal setae, or notopod with a bundle of winged capillary setae, on each side. Segment 3 is achaetous in adult *Decemunciger apalea*; however, small notopods with larval, hooded, flared (spatulate) notosetae or winged capillary setae are present in early stages. Adult worms have 13 thoracic setigers, the last 10 of which are uncinigerous, and 14 abdominal uncinigerous segments (Zottoli 1982). In addition, 4 pairs of smooth branchiae are present on the dorsal surface of segments 3–5. Refer to Zottoli (1982) for a more complete description of adult characteristics.

Larval and juvenile stages of *D. apalea* in this study are named according to the total number of segments bearing spatulate and/or capillary notosetae (setigers). Post-setigerous segments are those that follow these setigers and bear uncinigerous pinules (neuropodia with uncini). For adults the word setiger refers to any segment with setae of either the capillary or uncinuate type. The number of thoracic segments with both capillary notosetae and neuropodial uncini is a diagnostic feature of juveniles and adults but not larvae since larvae gain and lose setae during development, and the thorax is not fully formed.

Early Development

The eight female *D. apalea* with mature eggs in their body cavities ranged from 2.5 to 5.6 mm in length and from 0.5 to 0.7 mm in maximum width, whereas the 13 males with mature sperm ranged from 2.6 to 5.95 mm in length and from 0.42 to 0.7 mm in maximum width. Therefore, speci-

mens with the full complement of adult setigers and ranging from 1.3 to 2.45 mm in length are considered juveniles. Worms less than 1.3 mm in length and lacking the full complement of adult setigers are considered larvae. On this basis, 89 adults, 126 juveniles and 178 larvae were identified from the 393 whole specimens removed from Panel N31 (DOS 2) (Fig. 1). Sexually mature specimens of this species previously studied (Zottoli 1982) ranged from 3.6 to 6.3 mm in length and from 0.54 to 0.9 mm in maximum width.

8-Setiger Stage.—The 8-setiger stage (Fig. 2) is named for its eight segments bearing notosetae. Larvae with less than 8 setigers were not found. In the 8-setiger stage (Fig. 2), larval ciliary bands were not evident; a short, medial, ventrally ciliated tentacle protrudes from the mouth. A muscular ventral bulb is visible internally, just below the pharynx and above the lower lip. Pharynx, esophagus, stomach and intestine are visible through the transparent body wall. The digestive tract is filled with particulate matter as well as occasional *Xylophaga* larvae, suggesting that they feed in the manner described for *Hobsonia florida* by Zottoli (1974): “larvae begin feeding on microscopic plant and animal material at about the two-setiger stage by forcing material from the mud surface into the digestive tract through the action of the ventrally located buccal mass and by cilia on the upper lip.”

Prostomial and pygidial pigment spots are lacking. Fused segments 1 and 2 are situated immediately behind the prostomium. Segments 3–6 (setigers 1–4) bear 2 small dorsolateral notopods each with 1 spatulate (hooded, flared) seta (about 11 μm long, 6 μm maximum width) (Fig. 3A) and 1–2 smooth, winged, bilimbate capillary setae (about 25 μm long, 2 μm wide basally) (Fig. 3A). The number of smooth, winged, bilimbate capillary setae per notopod increases as the larva grows from the 8- to the 14-setiger stage (Table 1).

One uncinus (about 6 μm long) is em-

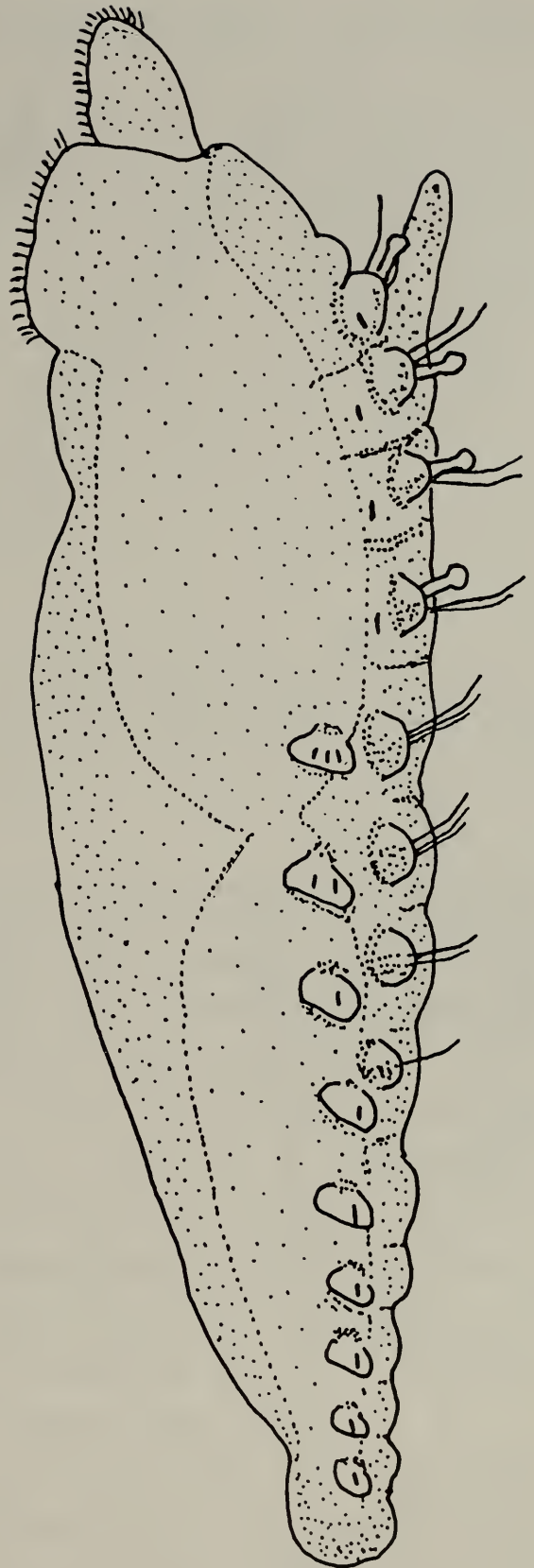


Fig. 2. *Decemunciger apalea* 8-setiger larva. Lateral view of entire worm, 0.6 mm long.

bedded in the epidermis, below the notopod, on each side of segments 3–6 (setigers 1–4). Each of the first 4 pairs of uncini have about 12 teeth above a basal prong (Fig.

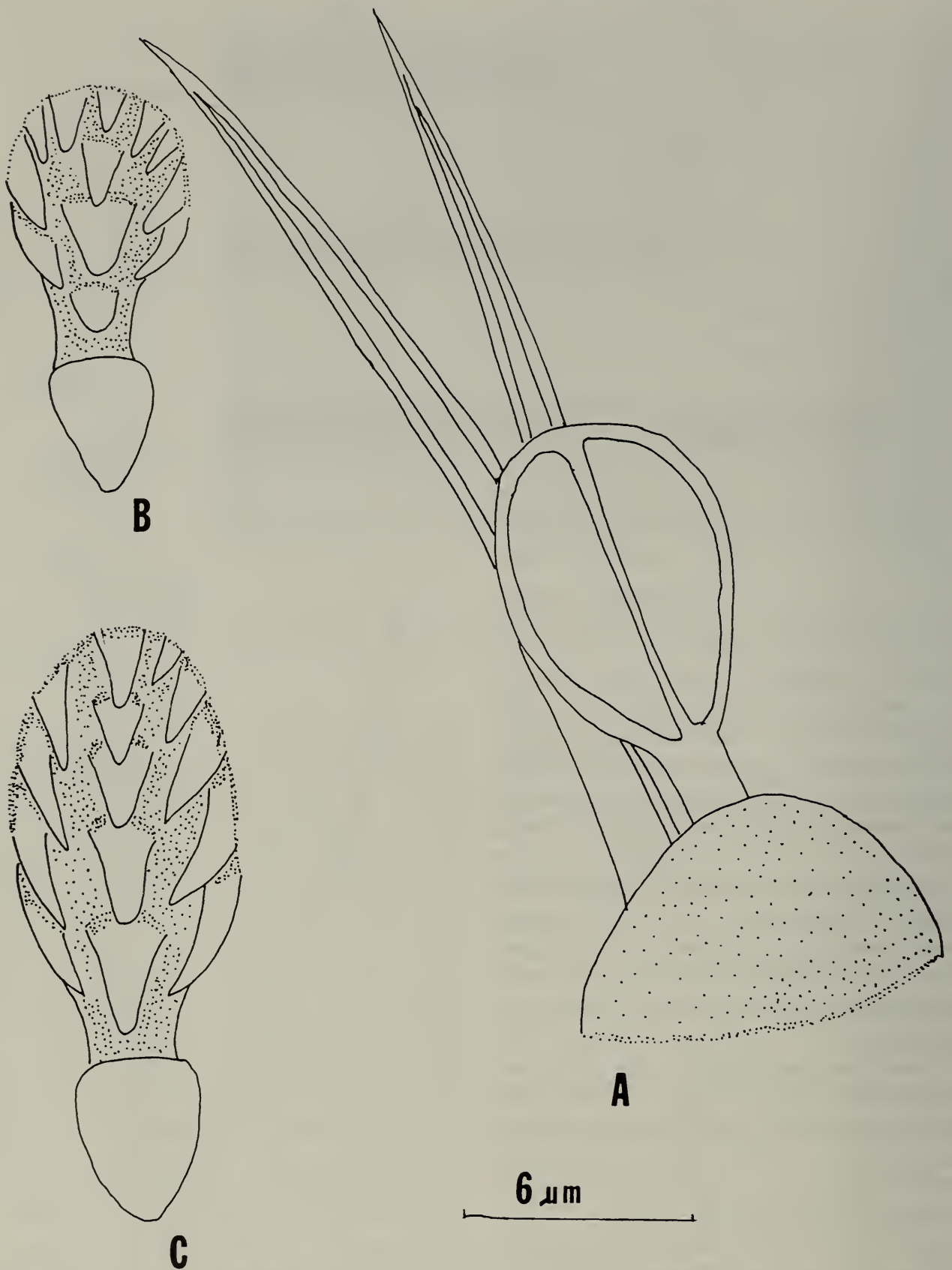


Fig. 3. *Decemunciger apalea* 8-setiger larva. A. Single spatulate seta and 2 smooth, winged, bilimbate capillary setae from the left notopod of the second setiger; B. Uncinus, frontal view, from the same setiger as above; C. Uncinus, frontal view, from the left uncinigerous pinnule of the 5th setiger.

Table 1.—Number of smooth, winged, bilimbate capillary setae per notopodium on “setigerous” segments of the 8- to 14-setiger stages of *Decemunciger apalea*. Note the loss of 1 setiger between the 14b- and 13a-setiger stages.

Segment	Setiger	Setiger stage								
		8	11	12	14a	14b	13a	13b	13c	13d
3	1	1	1	2	1	1	0	0	0	0
4	2	2	3	3	2	3	3	3	6	4
5	3	2	3	5	3	3	3	4	6	4
6	4	2	4	5	3	3	5	6	8	6
7	5	3	3	5	4	6	6	7	8	8
8	6	2	2	3	3	6	6	6	8	8
9	7	2	2	3	3	5	6	6	9	8
10	8	1	2	2	3	4	6	6	9	9
11	9		1	2	4	4	5	6	8	9
12	10		1	2	3	4	5	5	8	9
13	11		1	2	3	4	4	5	8	8
14	12			2	3	4	4	5	8	6
15	13				3	3	4	5	7	6
16	14				2	2	3	3	7	6

8 = 0.6×0.19 mm (1 pair br.), 11 = 1.0×0.19 mm (1 pair br.), 12 = 0.9×0.18 mm (2 pair br.), 14a = 1.4×0.28 mm (3 pair br.), 14b = 1.56×0.30 mm (3 pair br.), 13a = 1.75×0.30 mm (4 pair br.), 13b = 2.10×0.75 mm (4 pair br.), 13c = 3.50×0.50 mm (4 pair br.), 13d = 5.00×0.80 mm (4 pair br.), 14b = 1.56×0.30 mm (3 pair br.), br = branchiae.

3B); they disappear in later stages making segment 7 (setiger 5) the first uncinigerous thoracic segment in juveniles and adults. Segments 7–10 (setigers 5–8) bear 2 dorso-lateral notopods each with one or two smooth, winged, bilimbate capillary notosetae (about $25 \mu\text{m}$ long and $2 \mu\text{m}$ wide basally) (Fig. 2; Table 1). Uncini (about $8 \mu\text{m}$ long) from segments 7–15 (setigers 5–8 and postsetigers 1–5), are borne on ventrolateral extensions of the body (uncinigerous pinnules), one pair per segment (Fig. 2). Uncini have about 14 teeth above a basal prow (Fig. 3C). The numbers of uncini per uncinigerous pinnule on all setigers, except those of segments 3–6 (setigers 1–4) gradually increase from the 8- to the 14-setiger stage (Table 2).

There are 5 post-setigerous segments (segments 11–15) bearing uncinigerous pinnules but lacking notopodia and notosetae. The pygidium lies immediately behind segment 15. One pair of branchiae is present on the dorsoposterior edge of segment 3. There is a narrow mid-dorsal gap between the branchium of each side.

Larvae at this stage were found in membranous tubes covered by fine particulate matter. The membranous lining is most likely mucus secreted by the thick, glandular pads on the ventral surface of most thoracic setigerous segments.

11-Setiger Stage.—The 11-setiger stage (Fig. 4), named for its eleven segments bearing notosetae, is similar to the 8-setiger stage except for an increase in number of segments and setae (Table 1), an increase in length of the median tentacle, addition of 2 lateral tentacles, loss of larval spatulate setae on setiger 4, and loss of larval uncini on setigers 1 and 2 (Table 2).

12-Setiger Stage.—By the 12-setiger stage, named for its twelve segments bearing notosetae, the larval uncini on setigers 3 and 4 (Table 2), and the larval spatulate setae on setigers 1–3 disappear. There is an increase in the number of smooth, winged, bilimbate capillary notosetae per notopodium (Table 1) and in the total number of “setigerous” and “post-setigerous” segments (Table 2). There is an increase in the length of the median tentacle, and a second

Table 2.—Number of uncini per uncinigerous pinnule on “setigerous” and “post-setigerous” segments of the 8- to 14-setiger stages of *Decemunciger apalea*. Note the loss of 1 setiger between the 14b- and 13a-setiger stages. Stage lengths are listed in Table 1.

Segment	Setiger	Setiger stage								
		8	11	12	14a	14b	13a	13b	13c	13d
3	1	1	0	0	0	0	0	0	0	0
4	2	1	0	1	0	0	0	0	0	0
5	3	1	1	1	0	0	0	0	0	0
6	4	1	2	1	0	0	0	0	0	0
7	5	3	5	7	14	11	15	25	29	30
8	6	2	3	6	11	11	14	24	29	28
9	7	1	2	4	9	9	11	18	27	26
10	8	1	1	3	8	8	13	18	25	21
11	9	1	1	3	8	6	10	16	23	20
12	10	1	1	2	6	5	8	15	23	19
13	11	1	1	1	5	5	8	14	21	18
14	12	1	1	1	4	3	7	14	18	13
15	13	1	1	1	3	3	6	14	17	10
16	14		1	1	2	2	5	14	17	
“Post setiger” (Abdomen)										
17	15			1	2	2	3	5	16	10
18	16				1	2	3	5	10	10
19	17				1	2	3	5	10	9
20	18				1	2	3	5	8	9
21	19				1	1	3	5	7	9
22	20				1	1	2	5	7	6
23	21				1	1	2	5	7	7
24	22					1	1	5	7	5
25	23						1	5	5	4
26	24						1	4	5	4
27	25								4	4
28	26								2	3
29	27								3	

pair of branchiae appears on the dorsolateral, posterior surface between segments 4 and 5. Later, a third pair of branchiae arises from the dorso-lateral surface of segment 5.

14-Setiger Stage.—By the 14-setiger stage, all larval uncini on segments 3–6 have disappeared (Table 2, 14a, b). There is a general increase in the number of notosetae (Table 1) and uncini (Table 2). A fourth pair of branchiae arises from the anterior, dorsolateral surface of segment 6. Notosetae are eventually lost on segment 3, thus creating the 13-setiger stage described below (Table 1).

13-Setiger Stage.—The early 13-setiger stage (Fig. 5) (Tables 1–2, 13a) has the full complement of adult thoracic setigerous

segments of which 10 are uncinigerous. Uncinigerous thoracic segments begin on segment 7. Changes that occur between this stage and adult worms (Tables 1–2, 13c, d) include an increase in number of capillary notosetae per notopod, an increase in number of uncini per uncinigerous pinnule, an increase in number of teeth per uncinus to about 20, and an increase in number of uncinigerous abdominal segments to 12–14.

Uncini are first formed in the dorsal portion of each uncinigerous pinnule. They range in length from 6–8 μm in an 8-setiger stage to 6–13 μm in a 12-setiger stage and from 12–18 μm in a 13-setiger stage. As new, longer uncini are created, older,

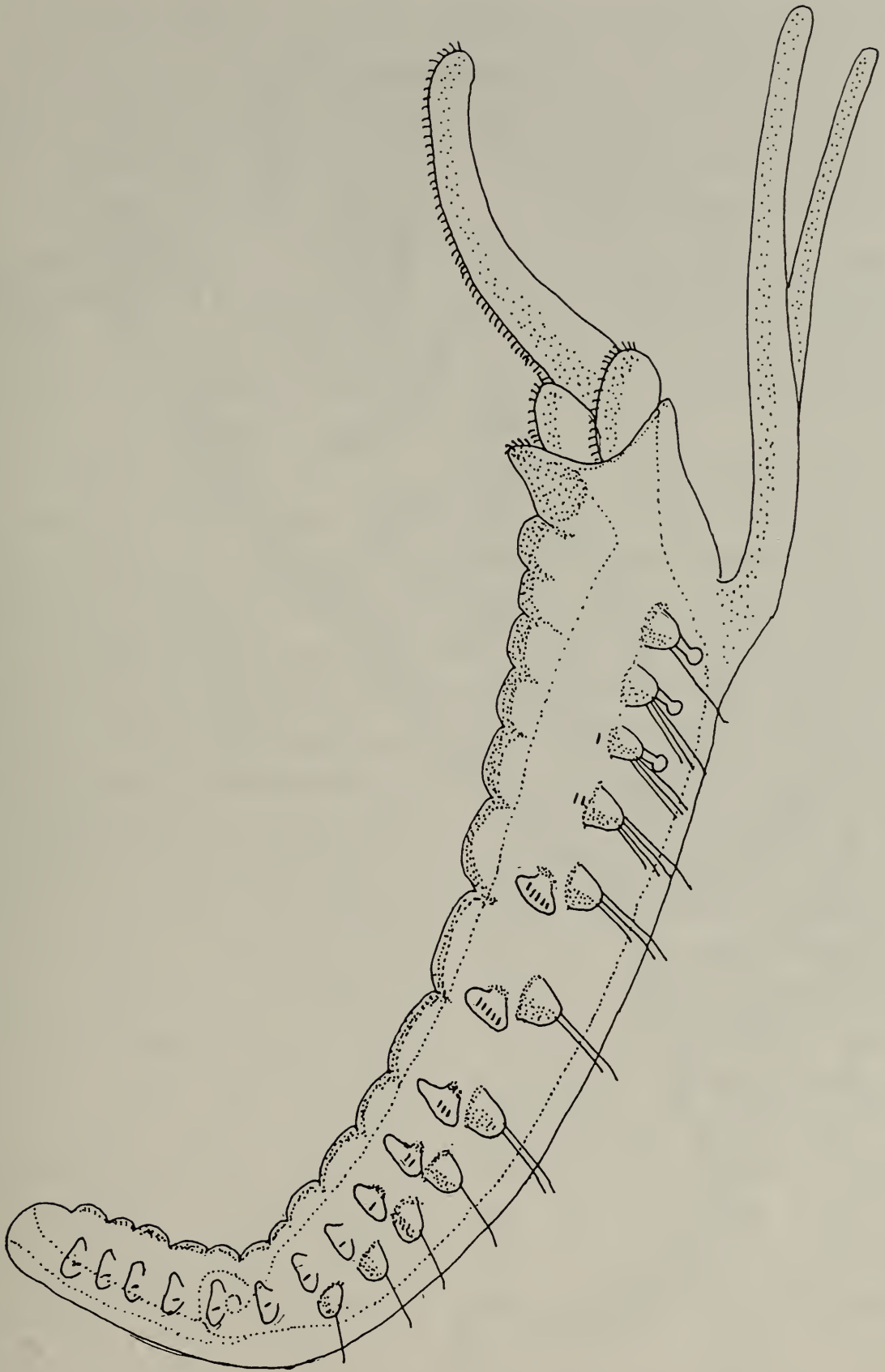


Fig. 4. *Decemunciger apalea* 11-setiger larva. Lateral view of entire worm, 1.0 mm long.

and shorter ones are pushed ventrally and eventually re-absorbed. This process is similar to that in *A. galapagensis* (Zottoli 1983) and *E. nebulosa* (Bhaud & Grémaré

1988). Few of the originally formed uncini remain in late juvenile and adult stages, suggesting an overall rapid growth rate for *D. apalea*.

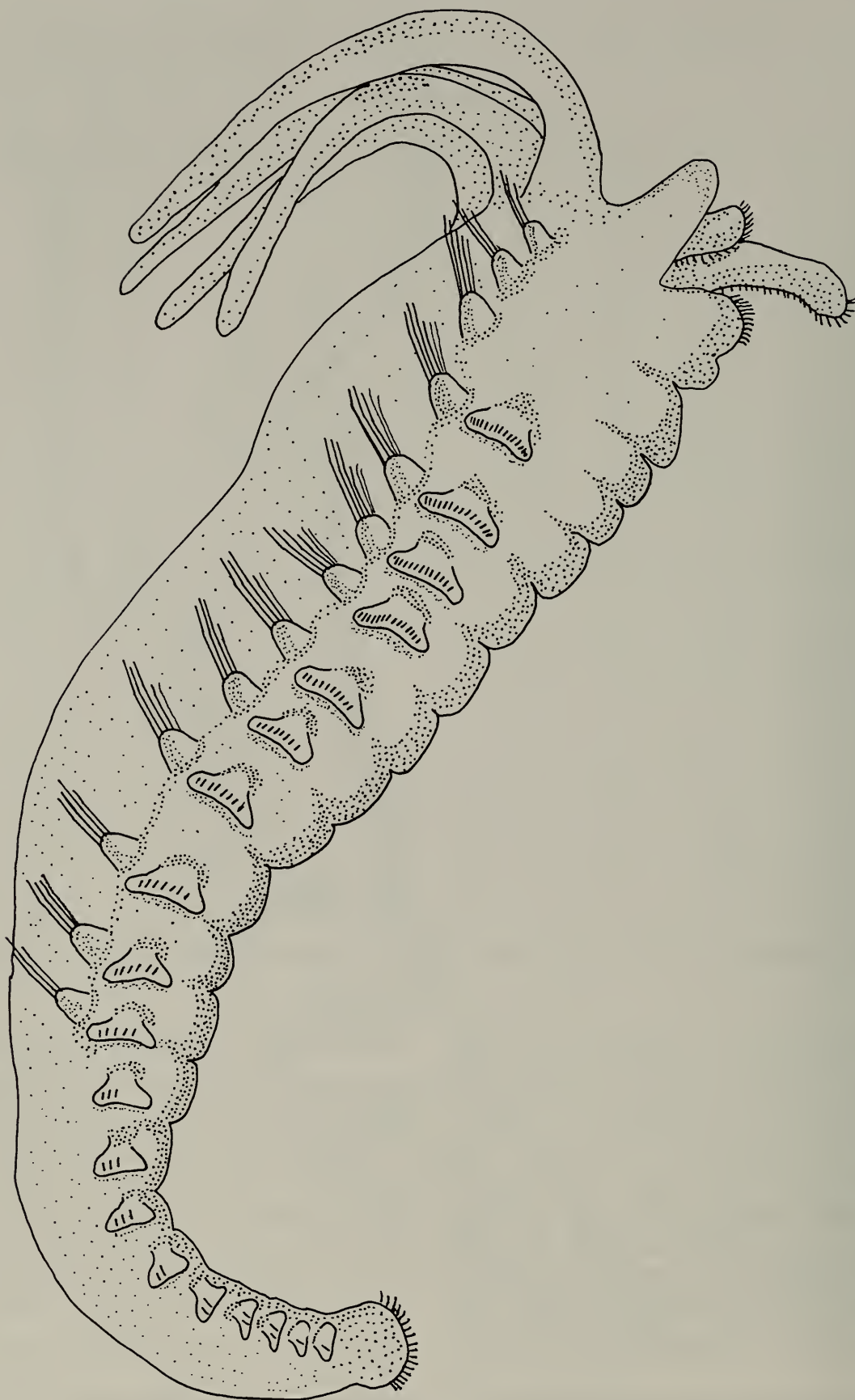


Fig. 5. *Decemunciger apalea* 13-setiger juvenile. Lateral view of entire worm, 1.75 mm long.

Discussion

Larval ciliated bands, although not found in *D. apalea*, disappear at about the 6-setiger stage in *H. florida* (Hartman) (Zottoli 1974), the 7-setiger stage in *Alkmaria romijni* Horst (Cazaux 1982), and were not found by Zottoli (1983) in later stages of *Amphisamytha galapagensis*.

Spatulate setae similar to those described in *D. apalea* are found in notopods of the first 3 setigers of larval *A. galapagensis* Zottoli (Zottoli 1983), *H. florida* (Hartman) (Zottoli 1974), and *Schistocomus sovjeticus* Annekova (Okuda 1947) and in the notopods of the first 4 setigers of larval *Ampharete acutifrons* (Grube) (Clavier 1984) and *Melinna palmata* (Grehan et al. 1991). What appear to be hooded, flared notosetae can be observed on Nyholm's (1950) photograph of a 3-setiger *Melinna cristata* Sars. Curiously, none were reported by Cazaux (1982) for *A. romijni*. Russell (1987) described hooded, flared setae in notopodia of segments 3–6 from the paedomorphic ampharetid *Paedampharete acutiseriens* Russell. He suggested that "the spatulate setae of *H. florida* and *A. galapagensis* may represent a type of "spatulate" setae distinctly different from that of *S. sovjeticus*, *A. acutifrons* and *P. acutiseriens*." A detailed examination of spatulate setae from larval *A. galapagensis*, *D. apalea*, and *H. florida* shows a similar 3-dimensional form to that described by Russell (1987). Notosetae, which are generally similar in appearance to ampharetid spatulate setae, have been described, respectively, by the bracketed authors on the first 6, 8 and 11 setigers of *Eupolymnia nebulosa* (Bhaud 1988 and Bhaud & Gremare 1988), *Thelepus setosus* (Duchêne 1983), and *Loima medusa* (Wilson 1928). Hooded, flared, notosetae eventually disappear, with the possible exception of *P. acutiseriens*, in all of the species discussed above.

The initial formation of spatulate setae, capillary notosetae and uncini and their subsequent loss on anterior segments here,

are generally similar to that described for the ampharetids *A. galapagensis* (Zottoli 1983), *M. palmata* (Grehan et al. 1991), *H. florida* (Zottoli 1974), and the terebellids *E. nebulosa* (Bhaud & Gremare 1988), *Loima conchilega* (Kessler 1963), *L. medusa* (Wilson 1928), and *Nicolea zostericola* (Eckelbarger 1974).

Larval and adult uncini are similar in *D. apalea*, in contrast to *A. galapagensis* (Zottoli 1983) and *H. florida* (Zottoli 1974) where multi-toothed larval uncini are replaced in most segments by uncini with a single row of teeth.

Branchial formation in *D. apalea* is similar to that of the ampharetids *A. galapagensis* (Zottoli 1983), *A. romijni* (Cazaux 1982), *H. florida* (Zottoli 1974), and possibly *P. acutiseriens* (Russell 1987).

Tubes, similar to those of *D. apalea*, were formed by 3-setiger, 1.75–2 day old *H. florida* larvae (Zottoli 1974), by 4-setiger *M. palmata* larvae (Grehan et al. 1991) and by 8-setiger, 20 day old *Alkmaria romijni* larvae (Cazaux 1982), shortly after they had abandoned the interior of the maternal tube. Larvae of the terebellids, *E. nebulosa* (Bhaud & Gremare 1988), *L. conchilega* (Kessler 1963), *N. zostericola* (Eckelbarger 1974), and *T. setosus* (Duchêne 1983), formed similar tubes, respectively, at the 6-, 2-, 14- and 4-setiger stages. Tube formation at such an early stage suggests that *D. apalea* larvae are benthic, remaining in the same general area as their parents. This does not preclude the possibility of larval transport from place to place by bottom currents. Once larvae form their own tube, they most likely remain permanently affixed, reaching new feeding areas by tube elongation as described by Fauchald & Jumars (1979). Eckelbarger (1974) reported that juvenile and adult *N. zostericola*, forced from their tubes, moved by repeatedly folding the abdomen upon itself and then straightening out. These actions lifted worms off the bottom and into the water column, transporting them short distances. The author observed similar movements in

juvenile and adult *H. florida* forced from their tubes. Because of the general similarity in body shape and structure of ampharetids and terebellids, it is assumed that most, including *D. apalea*, could move short distances in the manner described above if displaced from their tubes.

Panel N31 (DOS 2) was submerged for about 2 years from 5 Sep 1975 to 3 Aug 1977. There are more larvae and juveniles than adults (Fig. 1). Assuming that larvae and juveniles of *D. apalea* remain in the area where they were bred, Fig. 1 most likely reflects the distribution of the species as a whole. This assumption is supported by the fact that worms live in attached tubes in all but the earliest phases of their life and that their body shape is not conducive to sustained active locomotion in a pelagic environment. The presence of numerous larvae and adults with gametes in their body cavities suggests that breeding took place shortly before the time of retrieval. The small number of large adults suggests a life span of one year. This is also supported by the presence of gravid adults, juveniles and larvae in a panel (N68, DOS1) retrieved after approximately one year. If the life span of *D. apalea* were more than one year, one would expect a proportionately greater number of adults.

Acknowledgments

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